Exp Brain Res (1998) 118:408–414

RESEARCH NOTE

H. Chris Dijkerman · A. David Milner

The perception and prehension of objects oriented in the depth plane

II. Dissociated orientation functions in normal subjects

Received: 13 June 1997 / Accepted: 14 October 1997

Abstract Normal human subjects were tested for their ability to discriminate the orientation of a square plaque tilted in depth, using two different tasks: a grasping task and a perceptual matching task. Both tasks were given under separate monocular and binocular conditions. Accuracy of performance was measured by use of an opto-electronic motion analysis system, which computed the hand orientation (specifically, a line joining the tips of the thumb and index finger) as the hand either approached the target during grasping or was used to match the target. In all cases there was a very strong statistical coupling between hand orientation and target orientation, irrespective of viewing conditions. However, the matching data differed from the grasping data in showing a consistent curvature in the hand-target relationship, whereby the rate of change of hand orientation as a function of object orientation was smaller for oblique orientations than for those near the horizontal or vertical. The results are interpreted as reflecting the operation of two different mechanisms for analysing orientation in depth: a visuomotor system (assumed to be located primarily in the dorsal cortical visual stream) and a perceptual system (assumed to be located in the ventral stream). It may be that the requirements of visuomotor control dictate a primary need for absolute orientation coding, whereas those of perception dictate a need for more categorical coding.

Key words Visual perception · Visuomotor control · Orientation · Depth · Binocular vision · Human

Introduction

It is well established that cortical processing of visual information occurs broadly along two different routes, one terminating ventrally in the inferior temporal cortex, the other dorsally in the posterior parietal cortex (Underleider and Mishkin 1982; Morel and Bullier 1990; Baizer et al. 1991). The functional division of labour between these two systems, however, is more controversial. It was originally proposed that the ventral and dorsal streams subserved object and spatial perception, respectively (Ungerleider and Mishkin 1982). More recently, however, it has been argued that the functional distinction between the ventral and dorsal stream is not so much between "what" and "where" as between "what" and "how", i.e. between visual processing for perceptual purposes in the ventral stream and for the guidance of motor acts in the dorsal stream (Milner and Goodale 1993, 1995; Jeannerod 1994). Support of this view comes from well-documented dissociations between the use of visual information for perception and for motor acts in neurological patients. Optic ataxic patients are impaired when visually guiding their actions, while in many cases performing normally when using the same visual information for perceptual report (Levine et al. 1978; Perenin and Vighetto 1988; Jakobson et al. 1991; Jeannerod et al. 1994). Their brain lesions almost invariably include superior parts of posterior parietal cortex. In contrast, the visual-form agnosic patient D.F. has an incapacitating difficulty in the use of visual information for perceptual judgements, yet in many tasks shows normal visuomotor performance based on the same visual information (Milner et al. 1991; Goodale et al. 1991, 1994; Dijkerman et al. 1996). Her brain lesion includes dense bilateral damage to the lateral prestriate cortex (Milner et al. 1991).

The "what versus how" model would predict dissociations between performance on visuoperceptual and visuomotor tasks not only in brain-lesioned subjects but also in neurologically intact subjects. This expectation is based on the argument that the visual processing required for perceptual purposes is intrinsically different from that required for the guidance of motor acts. In general these differential needs will not cause a conflict, but occasionally they will. This is because the guidance of action requires coding of the instantaneous egocentric spatial location of objects and a snapshot of their physical attributes from the observer's viewpoint; while, in contrast, visual memory,

---

H.C. Dijkerman (✉) · A.D. Milner
School of Psychology, University of St. Andrews,
Fife, KY169 JU, Scotland, UK
Fax: +44-1334-463042, e-mail: hcd@st-andrews.ac.uk

served by the perceptual system, requires a more durable representation abstracted from the vagaries of the moment. One consequence of this latter need is that the perceptual system is subject to top-down influences from a visual knowledge base (Gregory 1997; Milner 1997) and as a result becomes a victim of perceptual illusions of space and size. For example, visual illusions such as the Titchener circles have been found to affect visuoperceptual size judgements much more than grip aperture during visuomotor grasping behaviour (Aglioti et al. 1995; Brenner and Smeets 1996).

A recent study has shown that the visual-form agnosic patient D.F. has greater difficulty in reporting the orientiation in depth of a target object than in adjusting her hand orientation when reaching out to grasp the object (which she performed at a completely normal level under binocular viewing conditions; Dijkerman et al. 1996). During that study, we noted certain peculiarities in the performance of the controls on the perceptual form of the task. The current paper reports a full study of this phenomenon, revealing a clear difference in normal subjects between perception and prehension of objects oriented in depth.

Materials and methods

Subjects

Six neurologically intact subjects (three men and three women), aged between 23 and 37 years, participated in the current study. All subjects were right-handed as assessed by the Edinburgh inventory (Oldfield 1971). Stereoacuity was examined with Frisby stereoplates and fell within the normal range for all subjects.

All subjects gave their informed consent to participate in this study. The study was part of an ongoing research programme for which ethical approval had been granted by the Tayside Committee on Medical Research Ethics.

Experimental setup

The apparatus used in the current study has been described in detail elsewhere (Dijkerman et al. 1996). The target object consisted of a square grey plastic plaque (5×5×1 cm) attached to a horizontal metal rod (30 cm long), which was mounted on a retort stand. The target object was placed 25 cm above the table surface. The base of the retort stand was situated 20 cm from the subject's starting hand position (a red spot located 6 cm from the near edge of the table). The target object could be rotated about the lateral-medial axis. Seven different orientations were used, varying from 0° (horizontal) to 90° (vertical) in steps of 15°. A second plaque identical to the target object was used in the perceptual matching task only. It was placed on the table, 12 cm from the starting position along the subject's mid-sagittal axis. A white background screen was placed on the side of the table opposite to where the subject was seated. The experimental setup is shown in Fig. 1.

Recording of movements

An Optotrak 3020 opto-electronic recording system (Northern Digital) was used to record hand movements and the orientation of the two objects. This system monitored the position of infrared-emitting diodes (IREDs) attached to the hand and embedded within the two objects, at a sampling rate of 100 Hz. Six IREDs were used in the visuomotor task and eight IREDs in the perceptual matching task. In both tasks, four IREDs were attached to the tips and to the most proximal joints of the subject's right index finger and thumb, and two IREDs were embedded inside the target object. For the perceptual matching task, the two additional IREDs were embedded in the second (hand-held) object. Data were collected for 3 s in the grasping task and for 1 s in the matching task. The data collection was also videotaped.

Procedure

Two different tasks were used, a visuomotor and a perceptual matching task. In both tasks subjects started each trial with their eyes closed, their head in a chin rest and with their right index finger and thumb held together (as in precision grasp) at the starting position. In the visuomotor task, on the experimenter's instruction, subjects were to open their eyes, reach out and grasp the target object

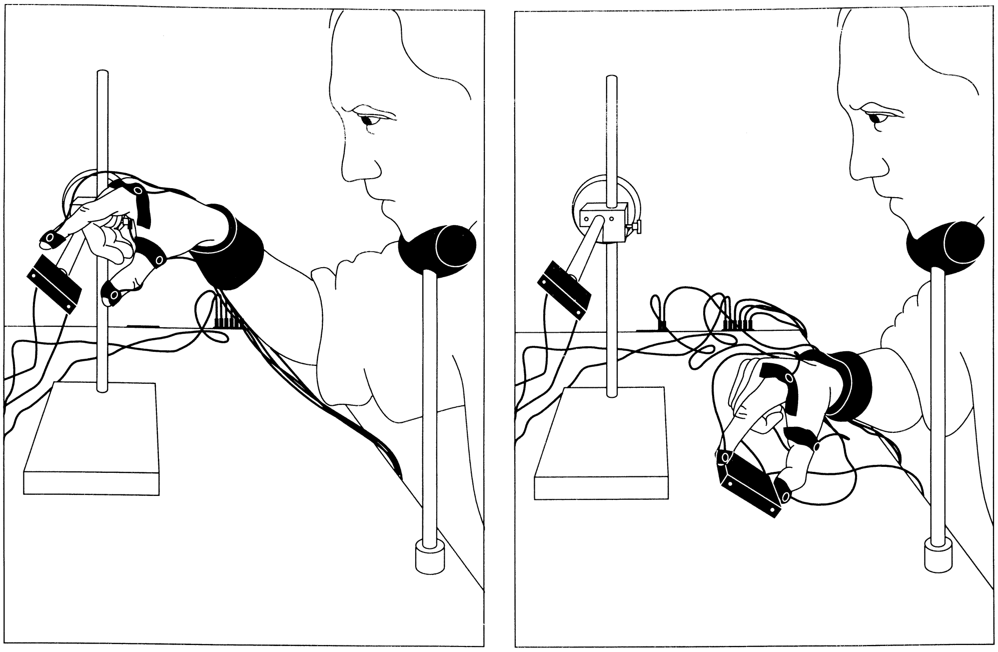

Fig. 1 The experimental setup for the grasping task (*left*) and the perceptual matching task (*right*)

front-to-back using a precision grip (i.e. index finger and thumb only; see Fig. 1, left). The whole movement was recorded using the Optotrak system. Although the target object could be removed from the stand, the subjects were instructed not to do so. The perceptual task was designed in such way that the type of response was as similar as possible to that used in the grasping task. The subjects were asked to perceptually match the orientation of the target object by grasping the second object (identical to the target object) placed in front of them on the table top, using precision grip, lifting it about 10 cm above the table surface and rotating it until its orientation was considered to be identical to that of the target object (see Fig. 1, right). Subjects thus made their responses in a different spatial location from the target, forcing subjects to code the stimulus in a perceptual (allocentric, viewpoint-independent) frame of reference rather than a visuomotor (egocentric, viewpoint-dependent) frame of reference (Milner and Goodale 1995). There were no time constraints and subjects were allowed to look back and forth between the target and hand-held objects as often as they liked. When the subject was satisfied that the orientation of the hand-held object matched that of the target object, the orientations of the hand and of the two objects were recorded for 1 s with the Optotrak system. A similar task, albeit devised for a different experimental purpose, was used by Soechting and Flanders (1993).

Each subject attended two sessions, one under binocular and one under monocular viewing conditions. Under monocular viewing conditions, an eye-patch was used to occlude the non-dominant eye. Three subjects were right-eye dominant, and three were left-eye dominant. The subjects were allowed to remove the eye-patch during the break between the block of trials for grasping and the block of trials for perceptual matching. All subjects performed the session in which binocular vision was available first. Within each session the visuomotor task was always carried out before the perceptual matching task. Each session contained 112 trials (56 matching and 56 grasping). Each of the seven orientations of the target object was presented eight times during each task within a session.

Data analysis

Since the angle of the target object was slightly variable for each set orientation, the angle between the line formed by the IREDs mounted within the object and the horizontal plane was calculated for each frame. Mean object angles were subsequently calculated over the whole duration of a trial and were used as the independent variable. Similarly, the angle of a straight line drawn through the IREDs on the index finger and thumb with respect to the horizontal plane was calculated for each frame. In the visuomotor task, the angle recorded two frames (20 ms) before contact with the object was used as the dependent variable. In the perceptual matching task, these index finger-thumb angles were averaged over the whole duration of the 1-s data collection period. A similar average was calculated for the angle formed by the two IREDs within the second (hand-held) object with respect to the horizontal plane. The data from the most proximal IREDs on the subjects' index finger and thumb were not used in the current analysis.

Results

Regression analyses

Binocular viewing conditions

For each subject, a mean hand orientation was calculated over all eight trials performed at each target orientation. Figure 2 (top) shows this mean hand orientation as a function of the mean target orientation for each of the six subjects. The grasping results plotted in Fig. 2a suggest that a linear regression line may fit these data best. This is borne

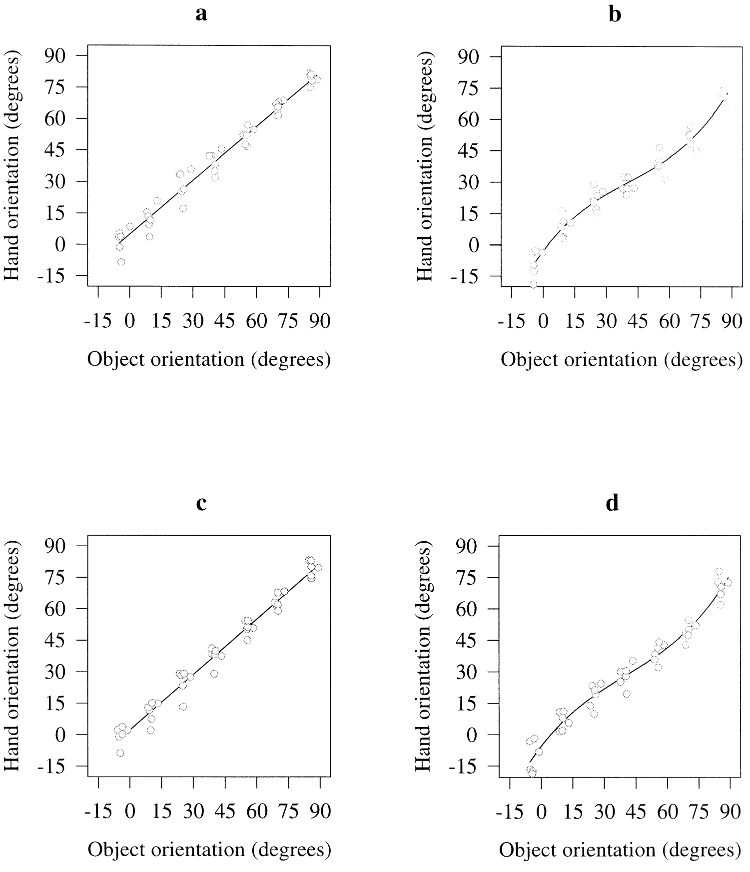

Fig. 2a–d Hand orientation as a function of object orientation for **a** binocular grasping, **b** binocular matching, **c** monocular grasping and **d** monocular matching. Each data point depicts the mean hand and object orientation of one subject

Table 1 Results of linear and cubic regression analyses on the binocular grasping and matching data. The results of these analyses were used to determine whether a cubic regression model would explain more of the variance than a linear regression model alone, using an *F*-test (*SS* sum of squares, *MS* mean square, *regr* regression, *res* residual, *diff* difference in $\mathrm{SS}_{\mathrm{regr}}$ between the 2 models)

		Binocular grasping	Binocular matching
Linear regression model	R^2	0.9713	0.9449
	Adjusted R^2	0.9706	0.9436
	$\mathrm{SS}_{\mathrm{regr}}$ (df=1)	28168.402	23970.435
	$\mathrm{MS}_{\mathrm{regr}}$	28168.402	23970.435
	$\mathrm{SS}_{\mathrm{res}}$ (df=40)	832.754	1396.595
	$\mathrm{MS}_{\mathrm{res}}$	20.819	34.915
Cubic regression model	R^2	0.9714	0.9600
	Adjusted R^2	0.9691	0.9568
	$\mathrm{SS}_{\mathrm{reg}}$ (df=3)	28171.676	24351.59
	$\mathrm{MS}_{\mathrm{regr}}$	9390.56	8117.20
	$\mathrm{SS}_{\mathrm{res}}$ (df=38)	829.48	1015.439
	$\mathrm{MS}_{\mathrm{res}}$	21.8284	26.7221
F-test	$\mathrm{SS}_{\mathrm{diff}}$	3.274	381.155
	$\mathrm{MS}_{\mathrm{diff}}$ ($\mathrm{SS}_{\mathrm{diff}}$/2 df)	1.637	190.5775
	$F_{2,38}=\mathrm{MS}_{\mathrm{diff}}/\mathrm{MS}_{\mathrm{res}}$	0.075*	7.132**

* n.s.; ** $P<0.005$

Table 2 Results of linear and cubic regression analyses on the monocular grasping and matching data. Again these results were used to determine whether a cubic regression model would explain more of the variance than a linear regression model, using an *F*-test

		Monocular grasping	Monocular matching
Linear regression model	R^2	0.9756	0.9538
	Adjusted R^2	0.9749	0.9527
	$\mathrm{SS}_{\mathrm{regr}}$ (df=1)	29470.177	26423.096
	$\mathrm{MS}_{\mathrm{regr}}$	29470.177	26423.096
	$\mathrm{SS}_{\mathrm{res}}$ (df=40)	738.738	1279.447
	$\mathrm{MS}_{\mathrm{res}}$	18.468	32.719
Cubic regression model	R^2	0.9759	0.9650
	Adjusted R^2	0.9740	0.9623
	$\mathrm{SS}_{\mathrm{regr}}$ (df=3)	29480.859	26733.506
	$\mathrm{MS}_{\mathrm{regr}}$	9826.9532	8911.1688
	$\mathrm{SS}_{\mathrm{res}}$ (df=38)	728.055	969.036
	$\mathrm{MS}_{\mathrm{res}}$	19.1594	25.5009
F-test	$\mathrm{SS}_{\mathrm{diff}}$	10.682	310.41
	$\mathrm{MS}_{\mathrm{diff}}$ ($\mathrm{SS}_{\mathrm{diff}}$/2 df)	5.341	155.205
	$F_{2,38}=\mathrm{MS}_{\mathrm{diff}}/\mathrm{MS}_{\mathrm{res}}$	0.279*	6.086**

* n.s.; ** $P<0.01$

Table 3 SDs of hand orientation (in degrees) for each object orientation within each condition. The SDs are averaged over the six subjects

	Binocular grasping	Binocular matching	Monocular grasping	Monocular matching
0°	5.26	2.31	3.95	3.50
15°	3.71	3.39	3.39	3.26
30°	4.32	5.04	4.47	3.74
45°	2.68	3.62	2.56	4.15
60°	2.96	3.84	5.33	4.96
75°	3.36	4.81	3.87	5.04
90°	3.54	3.53	4.14	4.34

out by the finding that 97.13% of the variance in the hand orientation data can be accounted for by the target orientation, merely by using a linear regression model. Analysis of variance showed that the linear relationship between target and hand orientation was highly significant on this grasping task ($F_{1,40}$=1353.02, $P<0.0001$). Fitting a quadratic or cubic regression model only negligibly increased the proportion of the variance explained (97.13% for quadratic, 97.14% for the cubic model).

The mean hand orientation when performing the perceptual matching task is shown as a function of mean object orientation for all six subjects in Fig. 2b. Inspection of this graph suggests that a cubic regression model might fit the data best. The variance explained by fitting a linear regression model alone is again highly significant (94.49%: $F_{1,40}$=686.54, $P<0.0001$). But while fitting a quadratic model does not increase the explained variance appreciably (94.50%), using a cubic model does result in a clear increase in the variance explained (96.00%).

Formal assessment of whether a cubic regression model would explain more of the variance in the data than a linear model was carried out using an *F*-test in which the restricted (linear) model was compared with the more general (cubic) model. In this test, the difference in the regression sum of squares ($\mathrm{SS}_{\mathrm{diff}}$) between the restricted and general model was used to calculate a mean square ($\mathrm{MS}_{\mathrm{diff}}$) by dividing $\mathrm{SS}_{\mathrm{diff}}$ by 2 *df*. An *F*-value was calculated by dividing $\mathrm{MS}_{\mathrm{diff}}$ by the MS of the residuals

(MS_{res}) for the more general (i.e. cubic) model. As shown in Table 1, a cubic regression model does explain significantly more of the variance in the perceptual matching data ($F_{2,38}$=7.13, P<0.005), but not in the grasping data ($F_{2,38}$=0.08, n.s.). Similar findings were obtained for the matching task when the orientation of the hand-held object itself was used as the dependent variable instead of hand orientation ($F_{2,38}$=9.87, P<0.005).

Monocular viewing conditions

The mean hand orientations as a function of object orientation under monocular viewing conditions for both the grasping and the matching task are shown in the lower part of Fig. 2. Again inspection of the data suggests that a linear regression model would fit the grasping data best, whereas a cubic model appears to be more appropriate for the perceptual matching data. This was tested using the F-test described above. Again, the cubic model did explain significantly more of the variance in the matching data than the linear model ($F_{2,38}$=6.09, P<0.01), but not in the grasping data ($F_{2,38}$=0.28, n.s.; see Table 2). The cubic model also explained significantly more of the variance in the matching data when the orientation of the hand-held object was used as the dependent variable instead of hand orientation ($F_{2,38}$=11.95, P<0.005).

Differences in variance

The regression analyses reported above show that on the matching task there is a smaller rate of change in performance as a function of target orientation across the oblique angles than at either extreme of the range (i.e. near the horizontal or vertical). This effect was not observed in the grasping task. One possibility is that the subjects were simply less consistent in their attempts to perceptually match oblique angles than horizontal or vertical angles. If so, this should also be reflected in the variance of the responses (i.e. there should be a larger variance in the matching responses to oblique target angles than to horizontal or vertical angles). To investigate this, the standard deviation (SD) over the eight responses for each of the object orientations was calculated for each individual subject separately. The SDs averaged across subjects are shown in Table 3. One-way repeated-measures ANOVAs were performed for each condition separately to assess whether there was any difference in mean SD of the hand orientation among the different object orientations. Significant differences were found for all conditions except monocular matching (binocular grasping: $F_{6,30}$=3.21, P<0.02; binocular matching: $F_{6,30}$=4.53, P<0.005; monocular grasping: $F_{6,30}$=2.77, P<0.05; monocular matching: $F_{6,30}$=1.77, n.s.). Post hoc analyses were performed with the Tukey test using a significance level of 0.05. For binocular grasping, SD of the hand orientation was significantly larger for object orientation 0° than for object orientation 45°; no other differences were observed. For binocular matching, SD of hand orientation was significantly smaller for object orientation 0° than for object orientations 30° and 75°; none of the other comparisons were significant. For the monocular grasping task, only the difference between object orientations 45° and 60° was significant with the SD being larger for the latter orientation. In summary, the possibility that subjects' responses were more variable at the oblique object angles on the matching task was not confirmed.

Binocular compared with monocular viewing conditions

Differences between binocular and monocular viewing conditions were assessed for the grasping task and the perceptual task separately. A repeated-measures ANOVA was performed for both tasks, with object orientation and viewing condition as within-subject factors and hand orientation as the dependent variable. For both tasks there was a highly significant effect of object angle ($F_{6,30}$=775.79, P<0.0001 for grasping; $F_{6,30}$=349.24, P<0.0001 for the matching task), but no significant effect of viewing condition ($F_{1,5}$=2.30, P>0.1 for grasping; $F_{1,5}$=0.81, P>0.1 for the matching task). The interaction between object angle and viewing condition was also not significant in either task ($F_{6,30}$=1.47, P>0.1 for grasping; $F_{6,30}$=1.07, P>0.1 for the matching task).

Discussion

The data of the current study show differences in the discrimination of object orientation depending on the task used. When reaching out to grasp an object oriented in depth, hand orientation increased linearly across all target object orientations. In contrast, during performance of the perceptual matching task, the rate of increase in hand orientation as a function of object orientation was reduced across the oblique object orientations (but not at the extreme – horizontal and vertical – orientations tested). A model including cubic regression therefore fitted the matching data better than a purely linear model. These data suggest that subjects are less able to distinguish perceptually between oblique object orientations than between object orientations close to horizontal or vertical. This phenomenon is reminiscent of the "oblique effects" often seen in studies of orientation discrimination in the picture plane (Appelle 1972; Caelli et al. 1983; Regan and Price 1986; Heeley and Buchanan-Smith 1990). However, we did not find any clear sign that the oblique orientations resulted in more variable judgements; rather the subjects tended to adopt a "default" oblique orientation in making their judgements, doing so in a fairly consistent manner. No such oblique effect was observed in the grasping task. Indeed hand orientation measured 20 ms prior to contact with the object increased strictly linearly with object orientation. (This was equally true in separate analyses carried out at 80 ms prior to contact.) This pattern of results adds to previously observed dissociations between visuomotor and perceptual performance, apparently reflecting different modes of processing of the same external visual information for different behavioural purposes (Bridgeman 1992; Aglioti et al. 1995; for review, see Milner and Goodale 1995).

As noted in the Introduction, one would expect that visuomotor performance would need to be controlled by absolute stimulus properties rather than by relative or categorical coding. It would not be useful for a visuomotor system to code an object's orientation merely as "oblique". In contrast, such coding would suffice for most purposes if one merely had to store the stimulus configuration for purposes of later recognition. If therefore our perceptual matching task is tapping coding processes whose normal function is to underlie visual recognition, then performance accuracy might be limited in the way we have observed as a result of such categorical processing.

It is now known that visual orientation in depth is coded in visual neurones in posterior parts of the intraparietal sulcus (Shikata et al. 1996; Sakata et al. 1997). We assume that these neurones provide a good part of the necessary visual input for guiding grasping in our task, and that the system lying more anteriorly in the intraparietal sulcus (area AIP), explored earlier by Sakata and his colleagues (Taira et al. 1990; Sakata et al. 1995), uses the outputs of such visual neurones in order to execute the visuomotor control itself. If this idea is correct, then it could be predicted that the orientation-selective neurones in the posterior area discovered by Shikata et al. (1996) should be distributed equally across all orientations in depth. By the same token, if the dissociation that we have discovered in the present study really does reflect the different processing characteristics of two separate cortical systems for analysing orientation in depth, then we must infer that the perceptual processing of oblique orientations, *ex hypothesi* in the ventral stream, is relatively less efficient. As yet there is no information on selectivity for orientation in depth in neurones within the occipito-temporal axis, still less on variations of such selectivity as a function of orientation.

Nonetheless, it is well known that there is binocular disparity information available in the ventral stream (Felleman and Van Essen 1987; Cowey 1994), and therefore neurones may exist that are orientation-selective in depth by virtue of such binocular inputs (like those studied by Shikata et al. 1996 in the posterior parietal cortex). In the case of the plaque used in the present study, the most effective metric to use in coding orientation might be shape disparity – i.e. a comparison between the shapes of the retinal projection of the plaque on the two eyes. But, in addition, it is likely that these ventral areas would use monocular cues for computing orientation in depth, such as perspective and texture gradients, as well as contextual information. This would help explain why patient D.F.'s hand orientation accuracy is greatly reduced when she grasps under monocular conditions (Dijkerman et al. 1996), while the accuracy of normal subjects is unchanged (Dijkerman et al. 1996; and this study).[1] We argued from those findings that normal individuals must be able to use added information about depth gradients derived from monocular form and surface cues, presumably processed within the ventral stream, when controlling their hand orientation, while D.F. cannot. It is also possible that our normal subjects used parallax cues (slight head movements would have been possible despite our use of a chin rest) for the control of hand orientation under monocular viewing conditions. A recent study by Marotta et al. (1995), however, found that normal subjects did not make larger head movements when grasping an object under monocular than binocular conditions. It remains most likely, therefore, that the subjects in the current study used form and surface cues, for which ventral-stream processing is presumably required. It will be interesting to see what light future physiological studies can cast on these putative ventral-stream mechanisms.

Acknowledgements We would like to thank A.D. Gordon and B.S. Pollard for their statistical advice, and D.P. Carey, L.K. Murray and C.L. Pritchard for their assistance with running the experiments. We are also grateful to A. Burnley for his expert technical assistance. This study was supported by a grant from the Wellcome Trust to A.D.M.

References

Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5:679–685

Appelle S (1972) Perception and discrimination as a function of stimulus orientation: the "oblique effect" in man and animals. Psychol Bull 78:266–278

Baizer JS, Ungerleider LG, Desimone R (1991) Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. J Neurosci 11:168–190

Brenner E, Smeets JBJ (1996) Size illusion influences how we lift but not how we grasp an object. Exp Brain Res 111:473–476

Bridgeman B (1992) Conscious and unconscious processes. The case of vision. Theory Psychol 2:73–88

Caelli T, Brettel H, Rentschler I, Hilz R (1983) Discrimination thresholds in the two dimensional spatial frequency domain. Vision Res 23:129–133

Cowey A (1994) Cortical visual areas and the neurobiology of higher visual processes. In: Farah MJ, Ratcliff G (eds) The neuropsychology of high-level vision. Erlbaum, Hillsdale, NJ, pp 3–31

Dijkerman HC, Milner AD, Carey DP (1996) The perception and prehension of objects oriented in the depth plane. I. Effects of visual form agnosia. Exp Brain Res 112:442–451

Felleman DJ, Van Essen DC (1987) Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. J Neurophysiol 57:889–920

Goodale MA, Milner AD, Jakobson LS, Carey DP (1991) A neurological dissociation between perceiving objects and grasping them. Nature 349:154–156

Goodale MA, Meenan JP, Bülthoff HH, Nicolle DA, Murphy KJ, Racicot CI (1994) Separate neural pathways for the visual analysis of object shape in perception and prehension. Curr Biol 4:604–610

Gregory RL (1997) Knowledge in perception and illusion. Philos Trans R Soc Lond Biol Sci 352:1121–1127

Heeley DW, Buchanan-Smith HM (1990) Recognition of stimulus orientation. Vision Res 30:1429–1437

Jackson SR, Jones CA, Newport R, Pritchard C (1997) A kinematic analysis of goal-directed prehension movements executed under binocular, monocular, and memory-guided viewing conditions. Vis Cogn 4:113–142

---

[1] It should be noted, however, that several other aspects of the prehension kinematics of normal subjects are altered by the unavailability of binocular vision (Servos et al. 1992; Servos and Goodale 1994; Marotta et al. 1995; Jackson et al. 1997).

Jakobson LS, Archibald YM, Carey DP, Goodale MA (1991) A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. Neuropsychologia 29:803–809

Jeannerod M (1994) The representing brain: neural correlates of motor intention and imagery. Behav Brain Sci 17:187–245

Jeannerod M, Decety J, Michel F (1994) Impairment of grasping movements following posterior parietal lesion. Neuropsychologia 32:369–380

Levine DN, Kaufman KJ, Mohr JP (1978) Inaccurate reaching associated with a superior parietal lobe tumor. Neurology 28:556–561

Marotta JJ, Perrot TS, Nicolle D, Servos P, Goodale MA (1995) Adapting to monocular vision: grasping with one eye. Exp Brain Res 104:107–114

Milner AD (1997) Vision without knowledge. Philos Trans R Soc Lond Biol Sci 352:1249–1256

Milner AD, Goodale MA (1993) Visual pathways to perception and action. Prog Brain Res 95:317–337

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, Oxford

Milner AD, Perrett DI, Johnston RS, Benson PJ, Jordan TR, Heeley DW, Bettucci D, Mortara F, Mutani R, Terazzi E, Davidson DLW (1991) Perception and action in “visual form agnosia”. Brain 114:405–428

Morel A, Bullier J (1990) Anatomical segregation of two cortical visual pathways in the macaque monkey. Vis Neurosci 4:555–578

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–114

Perenin M-T, Vighetto A (1988) Optic ataxia: a specific disruption in visuomotor mechanisms. Brain 111:643–674

Regan D, Price P (1986) Periodicity in orientation discrimination and the unconfounding of visual information. Vision Res 26:1299–1302

Sakata H, Taira M, Murata A, Mine S (1995) Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. Cereb Cortex 5:429–438

Sakata H, Taira M, Murata A, Gallese V, Tanaka Y, Shikata E, Kusunoki M (1997) Parietal visual neurons coding 3-D characteristics of objects and their relation to hand action. In: Thier P, Karnath H-O (eds) Parietal lobe contributions to orientation in 3-D space. Springer, Berlin Heidelberg New York, pp 237–254

Servos P, Goodale MA (1994) Binocular vision and the on-line control of human prehension. Exp Brain Res 98:119–127

Servos P, Goodale MA, Jakobson LS (1992) The role of binocular vision in prehension: a kinematic analysis. Vision Res 32:1513–1521

Shikata E, Tanaka Y, Nakamura H, Taira M, Sakata H (1996) Selectivity of the parietal visual neurons in 3D orientation of surface of stereoscopic stimuli. Neuroreport 7:2389–2394

Soechting JF, Flanders M (1993) Parallel, interdependent channels for location and orientation in sensorimotor transformations for reaching and grasping. J Neurophysiol 70:1137–1150

Taira M, Mine S, Georgopoulos AP, Murata A, Sakata H (1990) Parietal cortex neurons of the monkey related to the visual guidance of hand movement. Exp Brain Res 83:29–36

Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW (eds) Analysis of visual behavior. MIT Press, Cambridge, MA, pp 549–586

Valls-Solè J, Vila N, Obach V, Alvarez R, Gonzales LE, Chamorro A (1996) Brain stem reflexes in patients with Wallenberg’s syndrome: correlation with clinical and magnetic resonance imaging (MRI) findings. Muscle Nerve 19:1093–1099